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Animal Behavior: Timing in the Wild

A recent study has found that Rufous hummingbirds time the interval between successive visits to flowers that replenish at different rates. The hummingbirds have been shown to store information about both where and when they ate throughout the day, evidence that this species has two components of episodic memory.

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What do foraging hummingbirds (Figure 1) 'know' about the availability of food in their territory? A study by Henderson *et al.* [1], published recently in *Current Biology*, suggests that Rufous hummingbirds know when and where they recently encountered food. Free-living hummingbirds were found to time the interval between successive visits to eight artificial flowers that they visited throughout the day. This is the first evidence that hummingbirds in the wild remember when and where rewards occur and that they update this memory throughout the day.

In the new study [1], each flower was refilled with sucrose solution shortly after the bird emptied it. Half of the flowers were replenished after 10 minutes and the others after 20 minutes. The birds continued to revisit each flower throughout the day; however, they revisited the 10-minute flowers sooner than they revisited the 20-minute flowers. In order to revisit each flower at the right time throughout the day, the birds had to update their memories of when and where food was encountered for each flower.

Studies of time–place learning in animals — that is, their ability to discriminate when and where resources are available — have implicated two distinct ways of measuring time: circadian and interval timing [2]. Circadian timing involves a representation of the time of day, whereas interval timing involves estimating an elapsed duration with respect to an event, for example a previous reward.

A third hypothesis about temporal memory has also been proposed: according to this 'cognitive time travel' hypothesis [3], people mentally re-experience previous events from memory based on knowledge of when the event occurred in the past. Tulving [4] has argued that cognitive time travel is an essential component of episodic memory — the memory system that stores and retrieves one's unique, personal past experiences. Although cognitive time travel is a metaphor based on subjective experiences, it may be possible to develop quantitative models that subserve this type of temporal processing [2,5]. Cognitive time travel would enhance an animal's ability to compete effectively in foraging, predator avoidance and reproduction, so natural selection might thus favor the evolution of cognitive time travel. Moreover, insight into fundamental mechanisms of how the brain encodes and retrieves information may be obtained by studying memory in species that diverged from each other millions of years ago [6].

Knowledge of when and where represent two components of episodic-like memory. Clayton, Dickinson and colleagues [7,8] have argued that episodic-like memory can be documented in animals by demonstrating an integrated representation of when and where specific events occurred. They have shown that scrub jays have a detailed representation of when and where specific food types were stored. The proposal that non-human animals may have episodic-like memories is particularly interesting because it has long been assumed that this type of memory is unique to humans [3,4]. Henderson *et al.* [1] suggest that territorial hummingbirds may use episodic-like memories in their every-day lives, and thus hummingbirds represent a target for studying episodic-like memory.

Natural flowers differ in many features, and there would be a clear adaptive advantage for a hummingbird to be able to remember these features. Indeed, there is a growing body of

Figure 1. Rufous hummingbird (*Selasphorus rufus*).
Hummingbirds feed at numerous flowers throughout the day. Recent research by Henderson *et al.* [1] suggests that hummingbirds update a representation of when and where they fed after each visit. (Photo courtesy of Andrew Hurly.)

research that indicates that hummingbirds have a detailed representation of flowers that they encounter. This representation would appear to include information about color and pattern [9], spatial location [10,11], concentration and volume of food [12], and inter-reward interval [1,13]. This detailed representation makes the hummingbird a potentially useful model for investigating episodic-like memory.

But there are challenges that need to be addressed in developing a hummingbird model of episodic-like memory. The Clayton–Dickinson method for demonstrating episodic-like memory requires that the bird discriminate what, when and where. What type of a content component could be added to Henderson *et al.*'s [1] example of time–place discrimination? Although hummingbirds discriminate concentrations of food sources [12], concentrations of natural flowers probably do not fluctuate as a function of time; so it may be difficult to develop a naturalistic model using different concentrations.

Natural flowers do differ in terms of nectar volume, and the volume may be predicted by the amount of time since nectar was depleted [14]. Although volume is a promising direction for developing a naturalistic model of 'what–when–where', the birds' response to fluctuating volumes may represent a problem. Hummingbirds react to decreased volumes of food by markedly increasing the use of that food site for an extended period, for example one to two hours [13,15]. Although this pattern of behavior is an effective response to the competition that decreases nectar volume, this strategy may interfere with the expression of knowledge of what, when, and where.

Another potential challenge for developing a hummingbird model of episodic-like memory stems from the fact that local cues, such as food type, concentration, color and so on, are confounded with location in nature. Consequently, location may overshadow — that is, prevent learning about — content information [16,17]. Because location may serve as a sufficient cue to secure food, location may dominate over content when the birds learn to predict the availability of food.

A final challenge for developing a hummingbird model of episodic-like memory stems from the difficulty in ruling out alternative timing mechanisms. The cognitive-time-travel hypothesis requires that alternative timing mechanisms are ruled out. A circadian mechanism can be made irrelevant by ensuring that time of day cannot be used to solve the discrimination [7,18]. An interval-timing mechanism can be ruled out by showing that putative resetting cues are not used to time an interval [2]. But it may be difficult to establish that hummingbirds are not resetting an interval timer with respect to the presentation of food when relatively short intervals, for example 10 or 20 minutes, are used.

Episodic memory occurs late in human development, and it is the first type of memory to degenerate with age [19]. There is a critical need for animal models of episodic memory impairment because of the prominence of this problem in Alzheimer's disease and other common forms of human memory pathology. Recently, Babb and Crystal [18,20] have demonstrated discrimination of what-when-and-where in rats. Validation of a rodent model of episodic-like memory may facilitate future progress in understanding the neuroanatomical, neurochemical, and molecular mechanisms of episodic memory. Such a model would exploit the extensive knowledge about the neuroanatomy and neurophysiology of the rodent hippocampus, which is involved in episodic memory retrieval, and use neuroscience techniques to investigate the neuroanatomical, neurochemical and molecular bases of memory.

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